Ontario, Alberta, and British Columbia and there are annotated lists for substantial parts of the others. Nest record schemes administered by various federal and provincial agencies exist for all provinces.

Although Canada has been very active in ornithology, particularly since the late 1940's, much remains to be done: the ornithological exploration of the country has not yet been completed, taxonomic problems remain to be solved, various in-depth ecological studies are just beginning to yield stimulating results, and current behaviour studies are providing important new data.

We regret that we cannot mention here all ornithologists whose work is so deserving. We thank the following for various information: J. C. Barlow, F. G. Cooch, V. M. Humphreys, R. D. James, and Rev. R. C. Long.

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Fifty years of American Ornithology

by Robert E. Ricklefs and Frank B. Gill

Neither of us is approaching his 40th, let alone 50th birthday, and so our appraisal of the last 50 years of American ornithology is strongly influenced by current trends and our own interests*. Furthermore, as travel and communications between nations have increased, and as English has become the common language of science, differences in the expression of ornithological interest in different countries have faded and ornithology has become truly international. Yet many aspects of American ornithology have both developed independently and retained a distinctive flavour. We shall concentrate on these while giving credit where it is due to European influences on our endeavours. We shall also indicate what we believe are some ongoing changes in the character of American ornithology.

At the beginning of the twentieth century, American ornithology was preoccupied with coming to grips with its avifauna through taxonomic and distributional analyses. These studies were initiated within the natural history museums in Philadelphia, Washington, Boston, and New York. But the foundations of a new American ornithology also were being laid at this time, particularly by Frank M. Chapman at the American Museum of Natural History in New York. Not content with traditional faunistics, he began to blend evolutionary biogeography, speciation, and ecological associations into his studies of the Colombian (1917) and Ecuadorian (1926) avifaunas. Chapman assembled a staff at the American Museum whose vitality and productivity during the 1930's and 1940's shifted the centre of systematic ornithology from the Old World to the New World, but also influenced the development of ornithology more generally. This group included John Zimmer (studies of Peruvian birds, 1931 and following), James Chapin (*Birds of the Belgian Congo*, 1932), R. C. Murphy (*Oceanic Birds*

*For a more detailed and balanced statement, see E. Mayr, "Materials for a history of American ornithology," the Epilogue to E. Stresemann (1975), *Ornithology from Aristotle to the present.* Cambridge, Mass.: Harvard University Press.

of South America, 1936), Ernst Mayr (*Systematics and the Origin of Species*, 1942), and later Thomas Gilliard, Dean Amadon, and Charles Vaurie.

The new blend of ecology, speciation, and evolution that characterised American ornithology was gradually assimilated into American universities, beginning with the appointment in 1915 of Arthur A. Allen to a position as ornithologist at Cornell. Similar centres appeared at Berkeley with Joseph Grinnell and A. H. Miller, at Michigan with Jocelyn Van Tyne, and at Illinois with S. Charles Kendeigh. Their families of students are directly responsible for the flowering of ornithology in academic institutions in the United States and Canada. It is no accident that when 244 college and university professors, mostly in their 30's and 40's, responded recently to an AOU questionnaire concerning their graduate institutions, 40% had received their degrees from Berkeley, Illinois, Wisconsin, Michigan, and Cornell, with the remaining 60% spread thinly among 66 other institutions.

The development of ornithology within academic institutions produced such distinctive American contributions as studies on hybridization by Charles Sibley and Lester Short, on community ecology and diversity by Robert MacArthur, and on the ecology of territorial and mating systems by F. A. Pitelka, J. Brown, and G. Orians. These efforts, in which the influence of the University of California at Berkeley has predominated, are currently being expressed in applications of genetic analyses to the structure of populations, of the molecular biology of proteins and DNA to studies of phylogenetic relationships among species and higher taxa, and of evolutionary thinking to the study of behavioural ecology. This integrative approach to avian evolution and ecology has been supported by the development of new techniques, such as the use of vocal characters analyzed spectrographically, pioneered by W. J. Borror and applied by Wesley Lanyon, W. John Smith, and others, to studies of systematics, communication, song development, and population structure.

To a large degree, studies in ecology developed in parallel on both sides of the Atlantic. American ornithologists, especially Robert MacArthur and Gordon Orians, were greatly influenced by Charles Elton, David Lack, and John Crook. The intense interest of Americans in island biogeography also can be traced to influences from Great Britian, whose ornithologists have had an inordinate amount of access to islands.

North American contributions to avian physiology in the last 50 years match advances in systematics and ecology. From W. Rowan's classical work on the relation of the gonadal cycle in juncos to photoperiod, sprouted a variety of American studies on physiology and endocrinology, ranging from D. S. Farner and J. R. King's investigations of annual cycles, including moult, which raised the White-crowned Sparrow to the status of the laboratory mouse, to D. S. Lehrman's studies on endocrine control of behaviour in the Ring Dove, ornithology's laboratory rat. Another distinctively American direction in physiology was the comparative approach of George Bartholomew, William Dawson, and Knut Schmidt-Nielsen, whose studies of the physiological ecology of birds concentrated on problems of heat water, and salt balances in desert-inhabiting species, and the energetics of free-living birds. Among studies on the energetics of birds and their overall functioning within the ecosystem, all roots can be traced back to S. Charles Kendeigh, of the University of Illinois, and his student, Eugene P. Odum.

These increasingly theoretical or technological disciplines of ornithology have been matched by comprehensive life-history and population studies of colour-marked individuals. Margaret Nice's work on the Song Sparrow was a model study, followed by Harold Mayfield's on the Kirtland's Warbler and most recently by Val Nolan's invasion of the privacy of the Prairie Warbler. American ornithologists, particularly Alexander Wetmore and R. M. de Schauensee, characterised tropical American avifaunas in detail. Life-history studies of Neotropical birds, pioneered by Frank M. Chapman, were extended by Alexander Skutch in his remarkable, life-long, comparative study of the nest life of tropical songbirds.

Conservation is not a uniquely American enterprise by any means, yet there are few programmes anywhere that can match joint U.S. and Canadian efforts to understand, monitor, and manage populations of waterfowl, or to protect such endangered species as the Peregrine Falcon, California Condor and Whooping Crane. Our strong tradition of wildlife conservation may derive in part from the fact that industrialised society was late in coming to the Americas and encroachment on habitats and species have come largely within the period of widespread interest in wildlife. America's conservation conscience was greatly lifted by Aldo Leopold, who also helped to institutionalise wildlife studies, most notably at the University of Wisconsin.

Along with the development of scientific ornithology in the United States and Canada, contributions from amateurs and avocational ornithologists, professionally involved in other fields, also grew. Arthur Cleveland Bent, chronicler of American bird lives, was an amateur. Frank Chapman and Arthur Allen catalysed popular interest in birds, partly through personal appearances and partly through the use of bird photography in popular articles. Crawford Greenewalt's contributions to the physics of sound production in birds, the basis of iridescence in hummingbird feathers, and the aerodynamics of bird flight, and Frank Preston's theoretical considerations of the abundance and rarity of species, illustrate the coupling of avocational interest in birds with other professional expertise.

Early in this century, Frank M. Chapman began the tradition of Christmas Counts, organizing amateurs to census our wintering avifaunas. The 70 years of data now accumulated are a major resource for understanding bird population trends in the U.S.

Bird watching grew rapidly as a popular hobby with the publication of Roger Tory Peterson's system for field identification. Monitoring the spectacular spring and fall movements of North American breeding birds also became popular among amateurs, whose observations have become a major component of modern American ornithology. These efforts were highlighted by Frederick Lincoln's 1939 book *Migration of Birds*, and by George Lowery's work relating transgulf migration to weather and they are complemented by recent studies by William Keeton and Steve Emlen on homing and orientation, an area in which collaboration with European, especially German, ornithologists has been productive.

In recent years, certainly, the vast resources of American academic institutions, funding agencies, conservation organizations and popular press have made a big difference in the growth and character of American ornithology. Millions of dollars each year are spent on pure research, survey, husbandry,

and conservation of birds. Somewhere about 1000 professional ornithologists are employed by universities and colleges. Between 4000 and 5000 American college students take courses in ornithology each year, while hundreds of graduate students receive advanced degrees based on studies concerning birds. Serious amateur ornithologists number in the thousands (c. 4500 belong to the 3 major national ornithological societies) and recreational ornithologists with a deep concern for conservation and the conditon of the environment number in the millions. By sheer weight of membership and pages of publications, the American ornithological societies contribute disproportionately to the world supply of information concerning birds. American ornithology has thus grown from a few contributions from the major museums to a broadly-based discipline of academic, professional, amateur, and government involvement, unparalleled elsewhere in the world.

As ornithology has developed during the past 2 decades, its character also has changed. By elevating ornithological research to the status of a well-funded scientific discipline, government and academia have attracted considerable outside talent lacking the natural history background of earlier ornithologists. Many research programmes now focus upon problems of general interest to ecologists, ethologists, physiologists, and evolutionists, rather than upon problems specifically motivated by interest in birds. In the survey mentioned earlier, of 893 M.S. and Ph.D. theses written since 1970, 46% were in the area of ecology, 23% in ethology/behaviour, and 11% each in physiology and wildlife. The remaining 10% included the more traditional topics of anatomy, palaeontology and systematics.

The trend leading from systematics, anatomy, etc. to ecology and behaviour reflects the changing interest of students from taxonomically-oriented studies to question-oriented studies, and also the fact that systematic and anatomical work on birds is well advanced compared to other taxa. Furthermore, so little fossil material exists and genetic studies are so difficult that, for evolutionary problems, studies of birds are not attractive.

While modern trends in research on birds are certainly consistent with and appropriate to the interests of American science, they also have two important implications for American ornithology. The first is that the museum tradition is slowly dying. Although museums have vast resources for systematic, evolutionary and ecological studies, and Federal support of collections is increasing, it is difficult to find well-trained curators among today's students. This despite the fact that the kinds of background studies that have made birds so attractive as subjects of biological research were largely inspired from within the museum tradition. Certainly the prominent role that birds have played in the study of evolution, speciation, island biogeography, and community organization springs directly from the drawers upon drawers of specimens in museum cabinets—but students rarely go to the source anymore.

The second implication is that the gap between the professional and the amateur ornithologist is widening. This is inevitable as research comes to rely on more complicated, often quantitative techniques and addresses more erudite questions; it is also unfortunate because professional ornithologists often got their start as amateurs (we both did), whereas this is less and less often the case nowadays. In addition, the data gathered by amateurs on breeding bird densities, number of eggs, nesting success, and so on, plus

the insights gained through pleasant hours of birdwatching, have traditionally catalysed the scientific study of population biology, life-history patterns, ethology, and behavioural ecology. Practically the only facets of ornithology not cut by amateur ornithologists or by the natural history-museum tradition were anatomy and physiology.

Balancing these trends in ornithology are improving attitudes towards the application of scientific methods to studies of birds. Traditionally such studies were descriptive and subjective, their value coming from highly developed intuitions about nature. During the 1960's, as ornithologists began to rub shoulders with molecular and cellular biologists, there was a reaction against the old approach. Some ornithologists embraced numerical taxonomy and mathematical models of natural systems to the point that these tools became goals in themselves; but while much intellectual excitement was generated, many of the questions posed were not answered to general satisfaction, and great promise was largely unfulfilled. We are now witnessing 3 trends in avian studies that reflect a more mature and balanced attitude. First, students are learning again that the best inspiration is still to come from Nature herself. The new questions of the 1960's and 1970's primarily demonstrated how little we knew about birds. Theory is likely to provide useful inspiration only when it is founded upon a strong base of empirical knowledge, and models are only a way of expressing our understanding of nature and of suggesting tests of the validity of our inspirations, certainly not themselves a source of inspiration. Second, our students are becoming much more expert in the analysis and statistical interpretation of their data. The importance of this is that ornithologists are establishing a better sense of criteria for agreeing on statements about nature. Whereas in the past the existence of many purported patterns was the subject of intense debate, we now have better tools for picking apart relationships and assigning a level of statistical validity to them. Third, ornithologists are becoming experimentalists. Although there has been a long tradition of experimentation in physiology and behaviour, manipulations are being applied more and more in ecological and other field studies.

We are hopeful that a return to Nature for inspiration combined with more general agreement on what constitutes scientific progress will lead to a renewed flourishing of ornithilogical study in America, in which regard, we modestly suggest that no discussion of American ornithology would be complete without mentioning the important contributions of our own studies on development rates in birds and on the behavioural ecology of nectar-feeding birds.

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